A STUDY OF THE VEGETATION AND FLORISTIC AFFINITY OF THE LIMESTONE FORESTS IN SOUTHERN AND SOUTHWESTERN CHINA[1]

Xu Zhaoran[2]

ABSTRACT

Four thousand two hundred eighty-seven specific and infraspecific taxa in 1213 genera and 195 families of vascular plants are reported from the forests occurring on limestone outcrops in southern and southwestern China; the majority are from the provinces of Guangxi, Guizhou, and Yunnan. Data of natural conditions in the explored area, including geology, geography, meteorology, soil sciences, and vegetation, are presented. The flora is treated in 14 distribution types, for example, tropical elements total 69.1% of the flora, northern temperate 9.9%, East Asian 9.9%, and endemics of China 4.7%. Some genera, such as *Camellia*, *Eurya*, *Hydrangea*, *Rhododendron*, and *Symplocos*, are poorly represented in the limestone forests, while *Chirita*, *Excentrodendron*, *Paraboea*, *Platycarya*, and some other genera are endemic or very abundant in this kind of vegetation. About one-third of the species are endemic or dominant species in the limestone vegetation. Characterized by calciphiles, a "limestone flora" is a valid floristic category distinct from non-limestone floras, especially an acid-soil flora in the same region.

The flora of southern and southwestern China is well known for its richness in endemism and biodiversity (Wu, 1980), but the forests occurring on the limestone outcrops in the same region, known as limestone forests, are much less known in the literature. Wu (1980) reported some studies on the plant communities occurring on the limestone substrates in China, but no comprehensive surveys of the vegetation and flora of the limestone forests for the entire southern and southwestern portion of China were available before the present study began.

The current study was carried out from 1982 until 1987 as partial fulfillment of my master's and doctoral degrees at Sun Yatsen University in China, and it continued until recently with funding support from the World Wide Fund for Nature International and the Smithsonian Institution. Data summarized in this paper mostly were collected on my expeditions made from 1982 to recent years (Table 1), which resulted in about 8500 plant collections from forests occurring on limestone substrates, as well as a number of samples of rock and soil, and other data. A checklist of vascular plant species from Chinese limestone forests based on my collections and the literature was compiled (Xu, 1993).

The floristic analysis reported here is based on the published checklist (Xu, 1993). Although my surveys focused on the provinces of Guangxi, Guizhou, and Yunnan, the study results are representative of Chinese limestone forests because these three provinces contain typical Chinese karst landscapes (Fig. 1).

Limestone species are considered for this study to be those that occur on limestone substrates but may also occur on non-limestone substrates; limestone endemic species are those that occur exclusively on limestone substrates.

HABITAT CONDITIONS

China possesses the largest limestone area in the world, with pure carbonate substrates covering an area of 283,000 km² (Fig. 1). The majority of limestone outcrops related to this study lie on the slope from the Guangxi Basin to the Yungui Plateau, i.e., southwestern Guangxi, southern Guizhou, and southeastern Yunnan (Fig. 1, upper left corner),

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Table 1. Major limestone areas in Southern and Southwestern China surveyed.*

Province	Locality	Coordinate	Vegetation
Guangdong	Lianxian	24°47′N, 112°25′E	Secondary
	Yangshan	24°29′N, 112°41′E	Secondary
Guangxi	Baishe	23°54′N, 106°38′E	Secondary
	Jingxi	23°09′N, 106°25′E	Primary
	Liuzhou	24°29′N, 109°25′E	Secondary
	Longlin	24°46′N, 105°20′E	Primary
	Nandan	24°58′N, 107°33′E	Primary
	Ningming	22°07′N, 107°02′E	Primary
Guizhou	Anlong	25°08′N, 105°27′E	Primary
	Anshun	26°15′N, 105°55′E	Secondary
	Ceheng	25°00′N, 105°48′E	Primary
	Lipo	25°26′N, 107°52′E	Primary
	Xingyi	25°05′N, 104°53′E	Secondary
Yunnan	Funing	23°36′N, 105°36′E	Primary
	Guangnan	24°04′N, 105°04′E	Secondary
	Loping	24°52′N, 104°16′E	Secondary
	Maguan	25°00′N, 104°20′E	Primary
	Wenshan	23°22′N, 104°12′E	Secondary
	Xichou	23°26′N, 104°38′E	Primary

* Only those surveys in which Xu Zhaoran participated (1982–1993). There may be other kinds of vegetation around the locality that were not known to the surveyor(s). The primary vegetation was forest, but the secondary vegetation may be forests or thickets.

which accounts for 198,000 km² of pure limestone outcrops (70% of the total in China). Beautiful karst landscapes and numerous fantastic caves provide various ecological niches for plants and wildlife, as well as for tourism.

Chemical composition and geological ages of the carbonate substrates in China are summarized in Lu (1965). The substrates, mainly limestone and partly dolomite, are deposits from the Devonian to the Triassic, ca. 3000–50000 m thick.

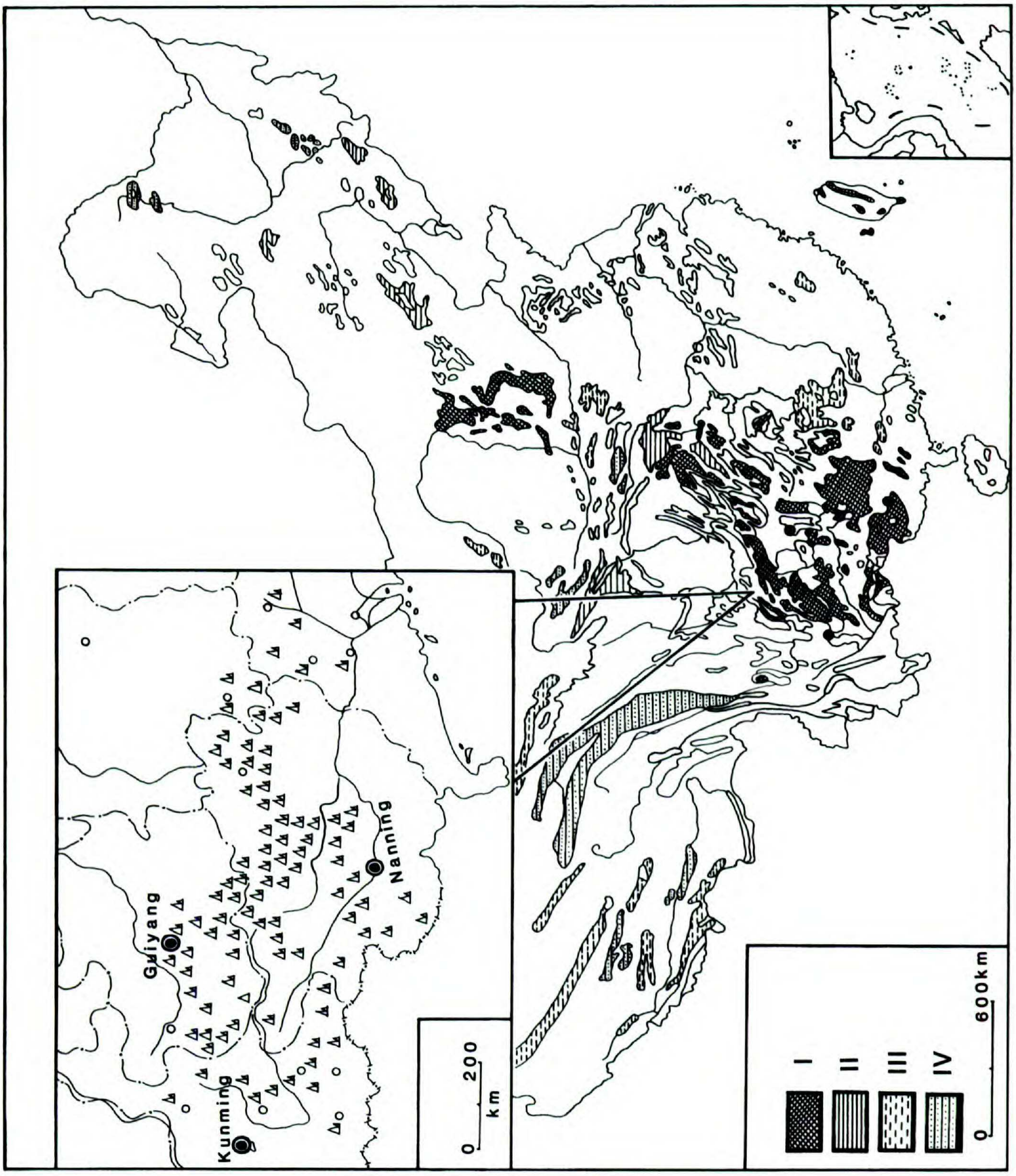
Rock samples collected during my expeditions (Table 1) were analyzed in Guangzhou Metallurgical Institute (Guangzhou), and the results show the following composition: calcium oxide (CaO) 50.00% of the total mass, magnesium oxide (MgO) 1.00%, aluminum (Al) trace value (less than 0.005%), manganese (Mn) 0.05%, silicon (Si) 0.01%, and iron (Fe) 0.10%. The above results indicate that the samples are limestone rather than dolomite, according to the classification of Lu (1965).

No contiguous soil layers have been found on pure limestone outcrops or karst hills, and it is unlikely that such soil layers can be formed there. According to Wei (1983), forming a 1-cm-thick soil layer on pure limestone substrates may take 13,000–32,000 years without accounting for leaching or erosion by rain. Because southern and southwestern China have a relatively high annual rainfall, and leaching or erosion is severe, soil deposits can only be found in crevices and pockets of rocks. More surface soil may be retained in limestone hills that are covered by forests than in those without forest cover.

Table 2 shows the chemical composition of some limestone soils. In subtropical areas under virgin forests (Number 3, Table 2), soil from rock crevices is black, with a high concentration of calcium (Ca^{+2}) but low aluminum (Al^{+3}), and the pH is around neutral (6–7). Soil collected from tropical localities with higher precipitation (Number 1, Table 2) may have lower pH values and lower concentration of Ca^{+2}. White soil (Number 2, Table 2) scraped from cliff surfaces has a pH value of 8–9, regardless of whether it was collected from a tropical area.

Some climate data are given in Table 3. The figures were gathered from local meteorological observatories in major collecting sites. In China, areas with an annual ≥10°C accumulated temperature[3] above 6500°C may develop tropical rainforests, and areas with an annual ≥10°C accumulated temper-

[3] The annual ≥10°C accumulated temperature is the total amount of temperature compounded from all the daily temperatures that are higher than or equal to 10 degrees Celsius in one year. This system is used in agriculture, forestry, and botanical research in China because a temperature of 10°C or above is considered to be effective for plant growth.


Guiyang
Nanning
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0 200 km
I
II
III
IV
0 600km

Table 2. Chemical composition of some limestone soil in Southern and Southwestern China.*

Climate zones	Vegetation and soil types	pH	% of dry weight								
			Mn	Fe	Mg	K	Ca	Al	Zn	Cu	P
Tropical	Number 1: brown soil (secondary forest)	5–6	0.46	9.24	0.45	0.46	0.68	12.0	0.04	0.01	0.26
	Number 2: white soil (on cliffs)	8–9	0.01	0.20	0.13	0.05	8.56	0.36	0.00	0.00	0.00
Subtropical	Number 3: black soil (primary forest)	6–7	0.15	2.20	0.39	0.29	1.38	2.17	0.02	0.00	0.02
	Number 4: brown soil (secondary shrubs)	5–6	0.06	7.65	1.30	0.29	0.37	13.5	0.02	0.00	0.09

* Soil samples were collected by Xu Zhaoran: Number 1, from Ningming, Guangxi; Number 2, from Maguan, Yunnan; Numbers 3 and 4, from Longlin, Guangxi. The samples were prepared and tested by Xu Zhaoran at the Testing Center of Sun Yatsen University.

ature of 4000 to 6500°C usually have evergreen broad-leaf forests. The former region is considered tropical, and the latter subtropical (Wu, 1980). According to Table 3, limestone areas in southern and southwestern China extend to both tropical and subtropical zones. Forests occurring on limestone substrates in the studied areas are a mixture of evergreen and deciduous broad-leaf forests, different from the regional evergreen forests described by Wu (1980). Details on the vegetation are presented in the following section.

Forest Vegetation

The limestone vegetation of southern and southwestern China can be divided into regions as diagrammed in Figure 2. Areas of particular botanical interest are southwestern Guangxi (I), southern Yunnan (II), Nanpan Jiang area (III), southeastern Yunnan (IV), southern Guizhou and northern Guangxi (V), and western Guangxi (VI). Central Guangxi (VII) and central Guizhou (VIII) are relatively developed areas without any remaining primary forests.

The solid line in Figure 2, which separates regions I and II from the others, is similar to the boundary of tropical and subtropical climatic zones. From the dotted line northward, the annual ≥ 10°C accumulated temperature (see Table 3) is generally less than 5000°C, and from this line southward, including regions III, IV, VI, and VII, the annual ≥10°C accumulated temperature is ca. 5000–6500°C, corresponding to south-subtropical climates. Thus, we may call the forest vegetation in regions I and II "tropical limestone forests," those in III, IV, VI, and VII "south-subtropical limestone forests," and those in V and VIII "middle-subtropical limestone forests." Regardless of what they are termed, the limestone forests are different from the non-limestone forests in the same regions in both their community structure and floristic composition. In regions I and II, trees may reach 70 m in height, and some trees of Dipterocarpaceae have been recorded as 70 m tall and 2 m diameter in both southwestern Guangxi and southern Yunnan. In III, IV, VI, and VII, the forest canopy may be as high as 30–40 m, but it is usually less than 25 m in V and VIII. In all these regions, deciduous trees form an important part of the upper layer of the forest, but in the middle layer there are more evergreen trees than deciduous ones.

The vegetation in the regions east of the vertical dashed line in Figure 2 differs from that west of the line. Floristic analysis of the collections from different sites indicates that many endemic species that occur in region IV are not found west of this region, while many endemic species recorded in

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Figure 1. Distribution of carbonate substrates and typical karst area (upper left corner) in China. In the main map, capital cities of the provinces of Guangxi, Guizhou, and Yunnan are represented by solid circles (Nanning, 22°50′N, 108°20′E; Guiyang, 26°34′N, 106°43′E; Kunming, 25°03′N, 102°43′E); in the insert (upper left), the corresponding cities are identified by name. Legends (bottom left): I, pure carbonate substrates. II, substrates of carbonate including small portion of noncarbonate. III, substrates of mixed carbonate and noncarbonate in similar portions. IV, substrates of noncarbonate including a small portion of carbonate. Translated and modified from the following two sources: Ren Meie & Liu Zhenzhong (1983): Outline of Karstology. Commercial Press, Beijing; and Academia Sinica (1980): Physiography of China, Topography. Science Press, Beijing.

Table 3. Some climate data of Southern and Southwestern China.*

Locality	Annual precipitation mm	Annual ≥10°C accumulated temperature °C	Yearly temperature °C	Monthly temperature		Yearly humidity %	Altitude m
				Lowest °C	Highest °C		
Hekou	1777	8249	22.6	15.3	27.5	85	137
Funing	1184	6401	19.3	10.9	25.2	79	>1000
Ningming	1350	7600	22.0	13.0	28.0	—	150
Libo	1300	4843	16.1	6.2	24.2	82	800

* Hekou, southern Yunnan; Funing, southeastern Yunnan; Ningming, southwestern Guangxi; and Libo, southern Guizhou. The annual ≥10°C accumulated temperature is the total temperature compounded from all the daily temperatures in one year that are higher than or equal to 10° Celsius (also see discussion in the text).

Xishuangbanna of southern Yunnan (Zhu, 1987) or region II are not present in the regions east of it, including regions I, IV, III and V (Chen, 1986; Liao, 1986; Liang et al., 1981, 1985; Xu, 1984, 1987).

Following are some characteristic species from the limestone vegetation in the above regions:

Southwestern Guangxi (I): *Amesiodendron chinense* (Merr.) Hu, *Cephalomappa sinensis* (Chun & How) Kosterm., *Cleistanthus saichikii* Merr., *Drypetes pereticulata* Gagnep., *Excentrodendron hsienmu* (Chun & How) H. T. Chang & R. H. Miao, *Garcinia paucinervis* Chun & How, *Parashorea chinensis* var. *kwangsiensis* Lin Chi, *Teonongia tonkinensis* Stapf, and *Walsura robusta* Roxb. Species of golden-flowered *Camellia* sect. *Chrysantha*, the so-called "giant pandas of the plant kingdom," are mostly found in this region.

Southern Yunnan (II): *Cleistanthus saichikii*, *Dracaena cochinchinensis* (Lour.) S. C. Chen, *Duabanga grandiflora* (Roxb.) Walp., *Horsfieldia* spp., *Parashorea chinensis* Wang Hsie var. *chinensis*, *Tetrameles nudiflora* R. Br., and some species of Combretaceae, Leguminosae, Meliaceae, Sapindaceae, and Sapotaceae that are often found in tropical rainforests.

Nanpan Jiang Area (III): *Carpinus* spp., *Celtis bodinieri* Lévl., *Chukrasia tabularis* var. *velutina* (Wall.) King, *Cleidiocarpon cavaleriei* (Lévl.) Airy Shaw, *Combretum alfredii* Hance, *Hiptage benghalensis* (L.) Kurz, *Koelreuteria bipinnata* Franch., *Pittosporum glabratum* Lindl., *Platycarya longipes* Y. C. Wu, *Quercus glauca* Thunb., *Sorbus purpurea* Z. R. Xu, and *Ulmus* spp. Region III is in the border area of the provinces of Guangxi, Guizhou, and Yunnan, and along the valley of Nanpan Jiang (River), which is the upper part of the Pearl River. It is interesting that even *Bombax ceiba* L., a tropical tree that is abundant in Vietnam, can be found here in some river valleys. The flora is a combination of eastern and western Chinese floristic elements.

Southeastern Yunnan (IV): *Burretiodendron esquirolii* (Lévl.) Rehd., *Carpinus pubescens* Burk., *Castanopsis fargesii* Franch., *Michelia fulva* Chang & B. L. Chen, *Miliusa chunii* W. T. Wang, *Pittosporum kerrii* Craib, *P. tonkinense* Gagnep., *Quercus glaucoides* (Schott) Rehd., and *Rapanea neriifolia* (Sieb. & Zucc.) Mez. Some species from regions I and III also appear in this region. In addition, there are some genera, such as *Calcareoboea*, *Malania*, and *Parepigynum*, that are endemic to southeastern Yunnan. This region is well known by its rich endemic and relict elements (Wu & Wang, 1985); it is especially rich in species of Magnoliaceae (Chen & Xu, 1993). I did not explore much of the neighboring western Guangxi (VI), because the limestone forests there are similar in vegetational and floristic composition to those in southeastern Yunnan; they differ in that fewer of them survive. In recent years, Wang (1990) recorded more than a hundred new species of Gesneriaceae in China, the majority of which were collected from one or a few limestone hills in western Guangxi. These species may indicate some distinctiveness between the floras of western Guangxi and southeastern Yunnan.

Southern Guizhou and northern Guangxi (V): *Acer sycopseoides* Chun, *Boniodendron minus* (Hemsl.) T. Chen, *Carpinus pubescens* Burk., *C. rupestris* A. Camus, *Clausena dunniana* Lévl., *Elaeagnus calcarea* Z. R. Xu, *Handeliodendron*

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FIGURE 2. Regionalization of major limestone vegetations in China: I, Southwestern Guangxi; II, Southern Yunnan; III, Nanpan Jiang area; IV, Southeastern Yunnan; V, Southern Guizhou and Northern Guangxi; VI, Western Guangxi; VII, Central Guangxi; VIII, Central Guizhou.

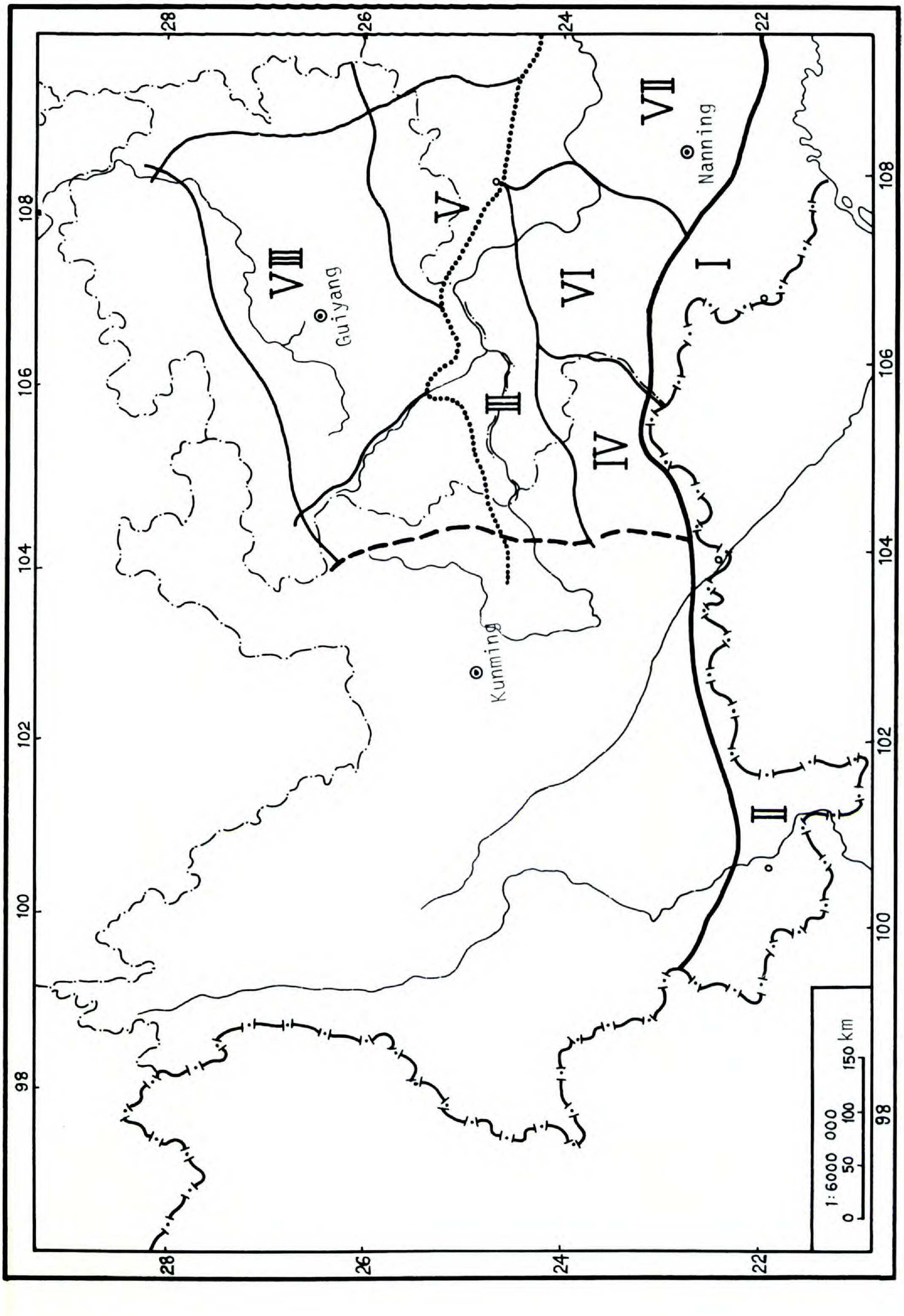
28
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Table 4. Size of the limestone flora of Southern and Southwestern China (Xu, 1993).

Plant group	Families	Genera	Species	Subspecies	Varieties	Forms
Pteridophyta	29	68	165	0	3	0
Gymnospermae	9	18	33	0	2	0
Angiospermae	157	1127	3778	11	271	24
(Dicotyledons)	(136)	(938)	(3263)	(11)	(239)	(22)
(Monocotyledons)	(21)	(189)	(515)	(0)	(32)	(2)
			3976	11	276	24
Total	195	1213		4287		

bodinieri (Lévl.) Rehd., *Keteleeria calcarea* Cheng & L. K. Fu, *Manglietia calcarea* X. H. Song, *Michelia angustioblonga* Law & Wu, *Pistacia chinensis* Bunge, *Pittosporum ovoideum* Gowda, *P. tetraspermum* Wight & Arn., *Platycarya longipes* Y. C. Wu, *Photinia tushanensis* Yu, *P. lochengensis* Yu, and *Pseudotsuga brevifolia* Cheng & L. K. Fu. Many of these species are endemic to southern Guizhou and northern Guangxi, where virgin forests on limestone hills have been found. A national limestone forest reserve was established in 1988 in southern Guizhou to protect the primary forests and wildlife. This reserve, where complete forest cover on the limestone hills extends for tens of kilometers, presents a rare case among the surviving limestone forests in southern and southwestern China. More than 50 new plant species have been reported from there in recent years (Xu, 1984, 1987; Zhou, 1987).

Fang & Liu (1984) claimed to have discovered an evergreen limestone forest in subtropical China (southern Sichuan). However, there are flaws in their report: (1) the forest is not on limestone hills or outcrops but on deep layers of soil from Quaternary deposits with a few limestone outcrops; and (2) the soil contains very low concentrations of calcium carbonate ($CaCO_3$), unlike that of limestone forests. In my years of extensive exploration throughout southern and southwestern China, I have found no evergreen forests on limestone outcrops or karst hills. Palynological studies of southern Guizhou limestone substrates provide evidence that the present limestone forest there is similar in floristic composition to the Tertiary flora of the same region (Zhou, 1987), suggesting that it is a primary forest. Our vegetation studies have shown that this primary forest is of mixed evergreen and deciduous trees (Xu & Sun, 1984).

Based on my sample studies, the limestone forests in southern and southwestern China are stable in population structure and differ from the acid-soil evergreen forests in the same region by: (1) having different dominant species, and the dominant species being less distinct; (2) possessing limestone-characteristic species (see Floral Features) of both evergreen and deciduous trees, especially in the upper layer of the forest; and (3) containing some tropical elements as well as some temperate elements that are seldom found in acid-soil forests in the same climatic zone or similar altitude.

It is important to point out that the limestone forests in southern and southwestern China have little similarity to arid floras, such as desert floras in tropical or subtropical areas in other parts of the world. As Table 3 shows, the region has relatively high precipitation. The degree of drought in this area is limited, and since aboveground streams can exist in limestone forests, aquatic or wetland plants can be found in this flora.

Floral Features

According to the checklist of limestone species (Xu, 1993), 4287 specific and infraspecific taxa of vascular plants have been recorded from the limestone forests in southern and southwestern China. They belong to 1213 genera and 195 families. Table 4 summarizes the size of the entire limestone flora of southern and southwestern China. Among the 195 families, 21 possess more than 50 species, which together account for 597 genera (49% of the entire flora) and 2111 species (53%) (Table 5). In the flora of China, these 21 families are also the largest families (Wu & Wang, 1985).

Following Wu (1981) and Wu & Wang (1985), the genera of spermatophytes of the limestone flora of southern and southwestern China are treated in 14 distribution types (Table 6). Compared with the flora of China as a whole (Wu & Wang, 1985), the limestone flora possesses a higher percentage of various tropical elements, including pantropical, disjunct in tropical Asia and tropical America, Old World tropic, tropical Asia to Australia, tropical Asia to tropical Africa, and tropical Asia (in total, 69.1% vs. 51.0%). Among the various tropical elements, the tropical Asian have the highest percentage (27.7%), which is also true in the Chinese flora (18.8%). This

Table 5. Families with more than 50 species in the limestone flora of Southern and Southwestern China. The arrangement of families is in order of the number of species.

Family	Gen.:Spp.	Family	Gen.:Spp.	Family	Gen.:Spp.
Leguminosae	52:224	Lauraceae	16:119	Acanthaceae	38:68
Labiatae	29:144	Rosaceae	23:112	Apocynaceae	28:63
Euphorbiaceae	50:142	Orchidaceae	38:106	Rutaceae	15:62
Rubiaceae	42:135	Liliaceae	17:100	Verbenaceae	10:61
Gesneriaceae	36:128	Moraceae	15:90	Vitaceae	7:57
Compositae	47:122	Gramineae	59:76	Araceae	17:56
Urticaceae	16:121	Asclepiadaceae	28:72	Annonaceae	14:53

result reflects the fact that the limestone area is located in the southern part of China within the tropical and subtropical zones, while the Chinese flora covers a large temperate area.

Although the limestone area is within the tropical and subtropical zones, the limestone flora includes 19.8% northern temperate and East Asian elements, a percentage comparable to that of the flora of China (20.7%). By critically examining the classification of Wu (1981), one can notice that southern and southwestern China are rich in temperate elements and are also the distribution centers of many tropical genera, such as *Annamocarya*, *Distylium*, *Eustigma*, *Camellia*, *Manglietia*, *Michelia*, *Kmeria*, and *Parakmeria*. The presence of so many temperate and tropical elements in the limestone forests in southern and southwestern China confirms that the area is rich in botanical diversity.

Since the majority of non-limestone substrates in southern and southwestern China can be roughly grouped into "acid soil," in which the soil pH appears acidic, my analysis will focus on the relationship between a limestone flora and an acid-soil flora.

Ninety-four families of vascular plants in the flora of China (IBASB, 1972–1983) have not been recorded from the limestone forests in the study area. This does not necessarily mean, however, that these 94 families occur only on non-limestone substrates in China, because limestone occurs elsewhere in China outside of the southern and southwestern portions of the country and because the

Table 6. Floristic analysis of spermatophytes of the limestone flora of Southern and Southwestern China in comparison with the entire flora of China (following Wu & Wang, 1985)

	Limestone flora		Chinese flora	
Distribution types	Genera	%	Genera	%
Cosmopolitan	49	—	108	—
Pantropical	183	16.7	372	13
Disjunct in tropial Asia and tropical America	31	2.8	89	3.1
Old World tropical	95	8.7	163	5.7
Tropical Asia to Australasia	70	6.4	150	5.2
Tropical Asia to tropical Africa	74	6.8	151	5.2
Tropical Asia	304	27.7	542	18.8
Northern temperate	108	9.9	296	10.3
Disjunct in East Asia and North America	34	3.1	117	4.1
Old World temperate	29	2.6	157	5.5
Temperate Asia	6	0.5	63	2.2
Mediterranean, West Asia to Central Asia	2	0.2	166	5.8
Central Asia	0	0	112	3.8
East Asia	108	9.9	298	10.4
Chinese endemic	52	4.7	196	6.8
Total	1145	100	2980	100 (99.9)

investigations of the limestone flora of southern and southwestern China are not complete. According to my personal observations, however, it is true that some of these families are abundant on acid soil, but never occur on the adjacent limestone outcrops, e.g., Bretschneideraceae, Clethraceae, Cyatheaceae, Gleicheniaceae, and Rhoipteleaceae. The Rhoipteleaceae are a monotypic family with a center of distribution in southern Guizhou, in which limestone outcrops are extremely common, but I have never documented any individuals of this family to occur in natural limestone habitats.

In general, large families may be distributed in more diverse habitats as well as more climate zones. But even some large families show a distinct difference in their patterns of distribution in limestone and acid soil. Ericaceae (ca. 800 spp.), Symplocaceae (80 spp.), and Theaceae (500 spp.) are three large families in the Chinese flora. Their distribution centers are actually in southern and southwestern China (Chang, 1980), but they have few representatives in the limestone flora (Ericaceae, 27 spp.; Symplocaceae, 6 spp.; Theaceae, 18 spp.). It is apparent that these families are well adapted to acid soil but not as suited to limestone. In Molan Natural Karst Reserve (southern Guizhou), I investigated the Symplocaceae and found only 2 individual plants that belonged to 2 different species in the limestone forests, while more than 20 species of this family are known to occur in acid-soil forests adjacent to the limestone reserve (Xu, 1984).

Contrary to the families that are well adapted to acid soil but not to limestone, the Chinese Gesneriaceae have a preference for limestone substrates. Among the 56 genera and 413 species of Gesneriaceae recorded in China, the majority were found on limestone outcrops or limestone hills, especially in the provinces of Guangxi, Guangdong, Guizhou, and Yunnan (Wang, 1990). Although Xu (1993) reported only 128 species of Gesneriaceae from limestone habitats, my personal collecting experience has convinced me that there are more gesneriad plants in limestone forests than in non-limestone forests. Many gesneriad species were not included in Xu (1993) because most of the available collections, other than those made by me, had no indication of habitat type; however, they probably had been collected from a limestone area. My recent monographic studies on some genera of Gesneriaceae support the theory that the family is well adapted to limestone habitats. The two gesneriad genera *Boea* and *Paraboea*, totaling more than a hundred species, are distributed from China to Southeast Asia and Australia and occur almost exclusively in limestone habitats (Xu & Burtt, 1991). Burtt (1984) and Chin (1977, 1979, 1983a, b) also recorded many Gesneriaceae species from limestone habitats in Southeast Asia. Besides Gesneriaceae, members of Euphorbiaceae, Juglandaceae, Pittosporaceae, Primulaceae, Rutaceae, Ulmaceae, and Urticaceae are apparently well adapted to limestone outcrops in southern and southwestern China.

Twenty-two genera, which are mostly monotypic or oligotypic and are confined to a small area, have been recorded as endemic to the limestone flora of southern and southwestern China, e.g., *Calcareoboea* (Gesneriaceae), *Excentrodendron* Chang & Miau (Tiliaceae), *Malania* Chun & S. Lee (Olacaceae), *Parepigynum* Tsiang & P. T. Li (Apocynaceae), and *Tengia* (Gesneriaceae). These genera represent trees, shrubs, lianas, and herbs, of which the herbal Gesneriaceae genera make up a large percentage. Most of these 22 genera have a distribution center in Guangxi, Guizhou, and Yunnan, which one might expect since the three provinces possess the majority of limestone substrates in China (Fig. 1).

There are a number of large genera characteristic of the limestone flora. Each large genus is not exclusively distributed in limestone habitats, but most of its species are endemic in the limestone flora. Examples include several Gesneriaceae genera, *Paraboea* (85 spp.), *Chirita* (130 spp.), *Hemiboea* (22 spp.).

In addition, some monotypic or oligotypic genera have been found to occur mostly in limestone habitats rather than in acid soil. Many of them have woody species that dominate the limestone forests in southern and southwestern China. Following are some examples, with the number of species recorded from the limestone forests in southern and southwestern China: *Burretiodendron* (4 spp., Tiliaceae), *Cephalomappa* (1 sp., Euphorbiaceae), *Delavaya* (1 sp., Sapindaceae), *Echinacanthus* (3 spp., Acanthaceae), *Pistacia* (2 spp., Anacardiaceae), *Platycarya* (3 spp., Juglandaceae), *Tetrameles* (1 sp., Datiscaceae), *Tetrathyrium* (1 sp., Hamamelidaceae), *Zenia* (1 sp., Leguminosae).

Contrary to the above genera characteristic of the limestone flora, some genera are characteristic of the acid-soil flora, with an abundance of species in acid-soil habitats, but few of their species occur in limestone forests within the same geographic region. These genera, though they do not represent the limestone flora, help reveal the relationship between a limestone flora and an acid-soil flora. Following are some examples; the numbers of species that have been recorded from limestone habitats versus those from acid-soil habitats in China are

listed in parentheses: *Camellia* (16:200, i.e., 16 spp. recorded in limestone area, while 200 spp. from acid soil; Theaceae), *Eurya* (0:80; Theaceae), *Hydrangea* (3:45; Saxifragaceae), *Pinus* (3:22; Pinaceae), *Rhododendron* (14:650; Ericaceae), *Symplocos* (6:77; Symplocaceae), and *Vaccinium* (8:45; Ericaceae). Although the current study focuses on southern and southwestern China, Xu (1993) had attempted to identify all of the Chinese limestone species of these genera by an exhaustive survey of the literature. The above ratio, therefore, may be taken as Chinese limestone species versus Chinese acid-soil species of the concerned genus. Within an acid-soil characteristic genus, there may be limestone characteristic sections or species. *Camellia* is a good example. Ninety percent of its species are found in acid soil, but the section of golden-flowered camellia, section *Chrysantha* Chang, is characteristic of limestone forests in southwestern Guangxi. Ten of the 15 species are exclusively distributed in limestone habitats, and the rest are exclusively distributed in acid-soil habitats, with only one exception that occurs in both acid-soil and limestone habitats (Ye et al., 1993).

Distinctions between a limestone flora and an acid-soil flora are best demonstrated at the species level. According to Chin (1977, 1979, 1983a, b), limestone species are classified into four groups in terms of their distribution patterns related to the limestone substrates: (1) *endemics*, species that are distributed exclusively in limestone habitats; this group comprises about 20% of the total number of species that have been recorded in the limestone flora in southern and southwestern China (Xu, 1993; the following percentages refer to the same source); (2) *preferents*, species that are more abundant on limestone, but rarely found on acid soil (about 10% of the species); (3) *indifferents*, species that show no distinct difference in their distribution in limestone and in acid soil; this group is the majority (about 65% of the species) in the limestone flora; (4) *strangers*, species that are more abundant in acid soil and seldom found on limestone (about 5% of the species). The endemics and preferents can be considered to be "limestone-characteristic species." More limestone-characteristic species may be found in a primary limestone forest than in a secondary one because human disturbance on a primary forest may eliminate some relict species, and, during recolonization in a limestone area, the relicts may not be able to return (Xu, 1986). These characteristic species are usually dominants in the limestone forests, regardless of whether they are trees, shrubs, or herbs that make up different layers of the forest.

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